Factors Affecting Egg Hatch, Development, and Survival of *Bemisia argentifolii* (Homoptera: Aleyrodidae) Reared on an Artificial Feeding System

J. L. BLACKMER,[1] L. L. LEE, AND T. J. HENNEBERRY

Western Cotton Research Laboratory, USDA–ARS, 4135 E. Broadway Road, Phoenix, AZ 85040

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ABSTRACT Improvements in the way *Bemisia argentifolii* Bellows & Perring is managed have led to reduced whitefly populations in the southwest United States. However, the potential of the silverleaf whitefly to develop new biotypes, as well as its apparently increasing role in virus transmission, makes it a persistent threat in many parts of the world. Characteristics such as biotype formation and vector competency are at least partially explained by the host range of *B. argentifolii.* Consequently, a better understanding of the factors that play a role in the host acceptance process and subsequent development of this pest could lead to novel control strategies. Here we used a newly developed artificial feeding system that consists of a polycarbonate chamber, equipped with a Teflon membrane, and filled with a sterilized artificial diet, to determine how biotic and abiotic factors influenced egg hatch, crawler establishment, and development of *B. argentifolii.* Egg age significantly influenced hatch rates, and to a lesser extent survival and development of nymphs reared on the artificial diet. Five- to six-day-old eggs had higher hatch rates, and nymphs survived longer and developed faster than nymphs from younger or older eggs. There were negative associations between the number of eggs placed on the membranes and both hatch rate and establishment of crawlers. Eggs oviposited on and then subsequently removed from plants held under long-day conditions (14:10 [L:D] h) or high light intensity (≈36,000 lux) had higher hatch rates than eggs oviposited under short-day conditions (10:14 [L:D] h) or low light intensity (≈11,000 lux). Long-day conditions during oviposition also significantly enhanced survival of nymphs through day 20 and developmental rate for day 6 counts. Light intensity, at least for the range tested here, did not significantly affect development or survival of whitefly nymphs.

KEY WORDS *Bemisia tabaci*, artificial diet, environmental parameters, oviposition, insect–plant interaction

DESPITE SUBSTANTIAL PROGRESS in the management of *Bemisia argentifolii* Bellows & Perring (Bellows et al. 1994), also referred to as *Bemisia tabaci* Gennadius (Biotype B) (Costa and Brown 1991), this insect continues to plague many parts of the world, causing millions of dollars in damage due to direct feeding or through its transmission of plant viruses. Renewed concern about the potential of *B. argentifolii* to disrupt agricultural production has occurred due to reports that new viruses are being transmitted by this insect (Banks et al. 1999; Abou-Jawdah et al. 2000; Brown 2000; Brown et al. 2000a, 2000b; Kao et al. 2000). These findings, as well as the potential *B. argentifolii* has for forming biotypes or host races (Brown et al. 1995) highlight the need for continued basic and applied research on whiteflies.

The development and identification of biotypes in insects has been associated with changes in host-plant range, host-plant acceptance and suitability, and vector-virus capabilities (Brown et al. 1995). A part of our research in the last few years has focused on determining the factors that play a role in whitefly host-plant selection, acceptance, and subsequent development. Previously, we demonstrated that as plant quality declined (Blackmer and Byrne 1993) and relative concentrations of certain phloem amino acids decreased (Blackmer and Byrne 1999), adult whitefly weights and emergence rates decreased, while developmental time from egg to adult and propensity to engage in long-distance flights increased. Our findings were important for generating hypotheses about how certain groups of amino acids might affect whitefly life-history traits, but because it is not easy to experimentally manipulate amino acid levels in the plant and extremely difficult to quantify trace metals, minerals and vitamins in phloem sap, a new approach was needed.

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[1] E-mail: jblackmer@wcrl.ars.usda.gov.

A recently developed feeding chamber designed to support whitefly development was used in our current studies (Jancovich et al. 1997, Davidson et al. 2000). A modified yeast extract diet and improvements in the feeder now enables a large percentage of the whitefly nymphs to develop to the fourth instar. This system has been used in gut-function studies (R. C. Rosell, University of St. Thomas, Houston, TX, and E. W. Davidson, ASU, Tempe, AZ, personal communications), for testing toxins (Jancovich et al. 1997), and for parasitoid/host interaction studies (Davidson and Jones 1999). Our ultimate use for the system is to develop a holidic diet that will support development of a substantial number of nymphs through to the adult stage. This system will allow us to experimentally manipulate dietary constituents and test hypotheses concerning the effect that particular amino acids, vitamins or trace metals and minerals have on whitefly host acceptance and suitability. Here we present findings on how several biotic and abiotic factors influence egg hatch and the success of whitefly nymphs on this artificial rearing system.

Materials and Methods

Chamber Setup. Whitefly feeding chambers were based on the design of Jancovich et al. (1997) with modifications as indicated in Davidson et al. (2000). The chambers consisted of an autoclavable, 45-mm-diameter TefSep Teflon laminated membrane with a pore size of 1.0 μm (Osmonics, Westboro, MA), sandwiched between two layers of polycarbonate plastic, which were held together by Father Time stainless steel binder clips (RPI, MT, Prospect, IL). The assembled feeding chambers were autoclaved at 120°C for 20 min and then exposed to a germicidal lamp in a laminar-flow hood for 30 min. Chambers were filled with sterilized diet, surface-sterilized eggs were placed on the membranes, and feeding areas were covered with glass slides to increase relative humidity. Feeding chambers were placed inside petri dishes that first had been treated with a 0.1% solution of miconazole (Sigma, St. Louis, MO) in 95% ethanol to inhibit fungal growth. To prevent eggs from drying out, sterile filter paper saturated with sterilized distilled water was added to each petri dish, the dish was sealed with Parafilm, inverted, and placed in a sealed plastic container in an environmental chamber maintained at 27 ± 2°C and a photoperiod of 14:10 (L:D) h.

Egg Sterilization Procedure. *B. argentifolii* eggs were harvested from young cotton plants, *Gossypium hirsutum* (L.) cultivar 'Delta Pine 5415'. Leaves were dipped sequentially into a detergent solution, distilled water, a 10% chlorine bleach solution for 2–3 min, to loosen the egg pedicel, and then doubly rinsed in distilled water. Eggs were washed off the leaves with a WaterPik dental device (Ft. Collins, CO), filtered through three layers of organdy cloth (6–8 fibers/mm), and collected on a coffee filter. From the filter, eggs were washed with distilled water into a 30-ml plastic centrifuge tube. Eggs were next put through a series of rinses: sterilized distilled water, 70% ethanol, 10% chlorine bleach solution for 2–3 min, and three sterilized distilled water rinses, that were each separated by centrifugation at 808–1043 × *g* for 1 min.

Diet Preparation. The diet for all experiments consisted of 5% yeast extract (BBL, Becton Dickinson, Cockeysville, MD) in 15% sucrose in distilled water. After all components were blended, the pH was adjusted to 6.5 using 1.75 M KOH. The diet was filtered through 25-mm diameter sterile syringe filters (0.2-μm pore size; Osmonics) before being placed in the feeding chamber well.

Effect of Egg Age and Number on Egg Hatch, Development and Survivorship. In preliminary trials, we noticed that egg hatch varied considerably once they were removed from the plant and placed on the membranes. We also observed that crawlers sometimes had a difficult time moving away from the eggshells upon emergence. To maximize hatch rates and establishment of crawlers, we examined the effects that egg age and number of eggs on the membrane had on these two parameters. Adult whiteflies were placed on clean cotton plants for a 24-h oviposition period and subsequently removed. Plants were maintained for 3–9 d in a Conviron growth chamber (model E8, Controlled Environments, Pembina, ND) at 27 ± 1°C, 50 ± 10% RH, 32,000 ± 1,800 lux at plant canopy level, and a photoperiod of 14:10 (L:D) h. Eggs for each age group were harvested and surface sterilized as described above. Six feeding chambers, each containing ≈167.5 ± 15.6 eggs, were set up for each age category. Eggs were evenly distributed over the surface of the membrane. The number of eggs placed on each membrane was counted on day 1, percentage of hatch was determined on day 5, and development and survivorship were monitored on days 5, 12, 18, and 25 after setup. Nymphs were recorded as dead when the body was flat and mycetomes were orange. Proportion data were normalized and variance equalized by arcsine of the square-root transformation before analyses. Survival percentage and developmental rates were compared by analysis of variance (ANOVA); and when the *F*-test was significant, means were separated by Bonferroni-*t*-test. For egg hatch percentage, variance was not equalized by the transformation, so these data were subjected to a Kruskal-Wallis ANOVA on ranks followed by Student-Newman-Keuls test for separation of means (SigmaStat 1994).

A varying number of eggs (<55 to > 600 eggs) were placed on the membranes of 61 feeding chambers to determine the effect that this had on egg hatch and crawler establishment. Eggs were evenly distributed over the surface of the membrane. Feeding chambers were held in an environmental chamber at 27 ± 2°C and a photoperiod of 14:10 (L:D) h. Eggs were counted on day 1, percentage of hatch was determined on day 5, and crawler mortality was determined on day 12. Day 12 mortality was due almost entirely to crawler mortality. The relationships between number of eggs, and egg hatch and crawler mortality were analyzed by regression analysis (SigmaStat 1994).

Effect of Photoperiod and Light Intensity on Egg Hatch, Development, and Survivorship. Over the course of our various trials, we noticed an ≈30% decrease in egg hatch and a slight delay in developmental rates that seemed to be associated with time of year. Therefore, the following experiments were designed to determine whether egg hatch and subsequent development were influenced by daylength or light intensity. Cotton seeds were germinated and plants maintained in an insect-free, climate-controlled (26 ± 3°C, 55 ± 20% RH, and a photoperiod of 10:14 [L:D] h) greenhouse until the plants had 7- to 15-true leaves. Young plants were watered and fertilized with a 50:50 mixture of all purpose Scotts Miracle-Gro Excel (Scotts-Sierra, Maryville, OH) (21–5-20) and cal-mag Miracle-Gro Professional (15–5-15) applied at a rate of 1 l/100 l of water by means of a tabletop capillary system. At the 7- to 15-true-leaf stage, plants were transferred to a second greenhouse, where they were placed on a drip-irrigation system. Temperatures, relative humidity, photoperiod, and fertilizer schedule were similar. Light intensity in both greenhouses was ≈50,000 ± 15,000 lux at plant canopy level.

Three weeks before trials were initiated, one set of plants (treatment = long-day, long exposure or LD:LE) was transferred to long-day conditions (14:10 [L:D] h) in a Conviron growth chamber (model E8, Controlled Environments) at 27 ± 1°C, 50 ± 10% RH, and 38,000 ± 2,000 lux at plant canopy level. After the acclimatization period, plants were placed inside cages within the Conviron, adult whiteflies were released, and allowed a 24-h oviposition period. A second set of plants was transferred to the Conviron just before the release of adults, so the plants were not acclimatized to long-day conditions, but adults oviposited on the plants under long-day conditions (treatment = long-day, short exposure or LD:SE). Twenty-four hours later, after adults were removed, the LD:SE plants were transferred back to short-day conditions (10:14[L:D] h) in the greenhouse. A third set of plants was maintained under short-day conditions during their development, as well as during the oviposition period (treatment = short-day, long exposure or SD:LE). For all treatments, plants were removed from the cages after the oviposition period. Five to six days later, eggs were harvested and surface sterilized as described above.

Eight feeding chambers, each containing ≈319.6 ± 18.8 eggs, were set up for each of the treatments. The trial was conducted twice. The number of eggs placed on each membrane was counted on day 1, hatch rates were determined on day 6, and development and survivorship were determined on days 6, 14, and 20 after setup. Data were analyzed as described previously.

In the light intensity study, when cotton plants had 7- to 15-true leaves, they were transferred to cages within the Conviron where they were allowed to acclimatize to long-day conditions for 3 wk. One set of plants was shaded with greenhouse shade cloth, so that light intensity was 11,620 ± 524 lux. A second set of plants, without shading, was maintained at a light intensity of 36,530 ± 892 lux. After the acclimitization period, adult whiteflies were released inside the cages, and allowed a 24-h oviposition period. Five to six days after the oviposition period, eggs were harvested and surface sterilized as described above. Ten feeding chambers, each containing ≈234.7 ± 10.0 eggs, were set up for each light intensity treatment. The trial was conducted twice. The number of eggs placed on each membrane was counted on day 1, and development and survivorship were determined on days 7, 14, and 21 after setup. Data were analyzed as described previously. Occasionally during the trials, chambers became contaminated with fungi or bacteria or diet leaked out, in which case they were eliminated from analyses.

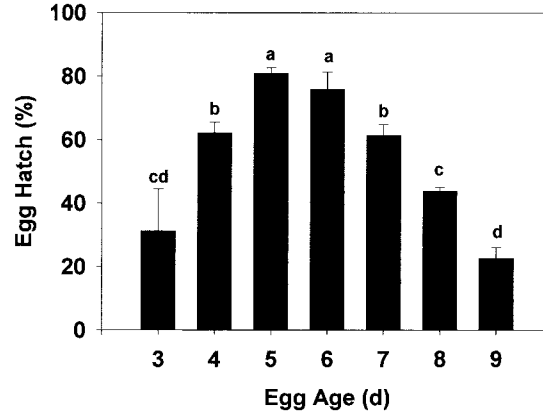

Fig. 1. Percentages of 3- to 9- d-old *B. argentifolii* eggs that had hatched by d 5 after removal from cotton plants and after being placed on Teflon membranes in an artificial feeding system. Different letters above bars indicate statistical significance (Student-Newman-Keuls test, $P < 0.0001$). Vertical bars indicate the SEM

Results

Egg Age Effect. For all egg age groups, ≈90% of the eggs that were going to hatch, had done so by day 5 counts. Five- and six-day-old eggs had significantly higher hatch rates than younger or older eggs (Fig. 1; $H = 31.0$, df = 6, $P < 0.0001$). At the time when eggs were washed off the plants, many of the 8- and 9-d-old eggs had already hatched, and for those eggs that remained on the leaf surface, hatch rates were relatively low (43.8 ± 1.3 and 22.6 ± 3.5%, respectively). Three-day-old eggs were more variable in percentage of hatch (31.2 ± 13.3%) when compared with all other age groups.

For comparisons of survivorship, 9-d-old eggs were excluded from the analysis because of the low number of eggs and low hatch rates. At day 5, there were no significant differences in survival among nymphs reared from different aged eggs, but in subsequent counts, nymphs from 5- and 6-d-old eggs, survived significantly better than nymphs from older eggs. This difference was most evident for day 18 counts (Fig. 2; $F = 6.18$, df = 5,25, $P = 0.0007$).

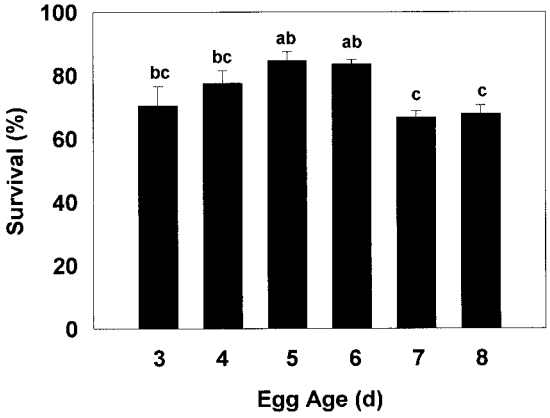

Fig. 2. Percentages of *B. argentifolii* nymphs that survived to d 18 from 3- to 8-d-old eggs that were placed on Teflon membranes in an artificial feeding system. Different letters above bars indicate statistical significance (Bonferroni-*t*-test; $P < 0.05$). Vertical bars indicate the SEM

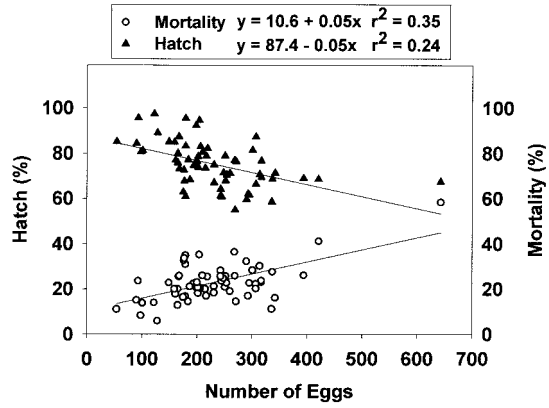

Fig. 3. Relationship between numbers of *B. argentifolii* eggs placed on an artificial feeding system, and percentage of hatch and mortality of crawlers on d 5. $P < 0.05$ in both cases.

When the percentage of nymphs developing to or beyond the third stadium was compared among age groups, nymphs from 3-d-old eggs were less likely to reach the third or fourth stadium in comparison with all other age groups for day 12 ($F = 6.49$; df = 5, 25; $P = 0.0007$) and day 18 counts ($F = 5.58$; df = 5, 26; $P = 0.001$). By day 25, nymphs from 3-d-old eggs were less likely to reach the third or fourth stadium in comparison with nymphs from 5-d-old eggs ($F = 3.10$; df = 5, 22; $P = 0.03$; Table 1). Emergence to the adult stage was highest for nymphs that emerged from 4-, 5-, and 6-d-old eggs (4.3, 6.5, and 2.8%, respectively), when compared with other age groups (0.7–1.1%) at day 25 counts. The highest rate of emergence to the adult stage from any single feeding chamber was 11.6%.

Egg Numbers on Membrane. Percentage of egg hatch and establishment of crawlers on TefSep (Osmonics, Westboro, MA) membranes were negatively influenced by an increasing number of eggs on the membrane. Egg hatch decreased ($F = 18.0$; df = 1, 59; $P < 0.0001$) and crawler mortality increased ($F = 31.5$; df = 1, 59; $P < 0.0001$) as the number of eggs increased (Fig. 3). This effect was due mainly to clumping of eggs, and the inability of the crawlers to move away from such areas. For crawlers that settled and fed on the membranes, no significant differences in development or survival were noted.

Photoperiod Effect. Hatch rates were significantly higher for eggs that were oviposited on plants exposed to long-day conditions over a 3-wk period or for the 24-h oviposition period only, in comparison with hatch rates for eggs from plants maintained under short-day conditions (Table 2). Similar to hatch rates, percent survival through day 20 counts was consistently higher for nymphs that emerged from eggs taken from plants held under long-day conditions, for both exposure periods, in comparison with nymphs that came from eggs taken from plants held under short-day conditions (Table 2). The only significant differences in development were seen at day 6 counts (Table 2). There were significantly fewer first instar and more second instar *B. argentifolii* for the feeding chambers that were set up with eggs from LD:LE plants than for either LD:SE or SD:LE plants. There were no significant differences in the percentage of nymphs that progressed to or beyond the third stadium for day 14 or 20 counts among the three plant treatments.

Light Intensity Effect. Hatch rates were significantly higher for eggs that were deposited on plants exposed to high light intensity in comparison with hatch rates for eggs from plants held under low light conditions (Table 3). However, there were no differences in survivorship or in development of nymphs at days 7, 14, or 21 due to light intensity (Table 3).

Table 1. Mean percentages (±SEM) of *B. argentifolii* that developed to or beyond the third stadium by days 12, 18, and 25 following hatch from 3- to 8-d-old eggs placed on Teflon membranes over artificial diet cells

Counts, d	Egg age when removed from plants					
	3	4	5	6	7	8
12	11.3 ± 7.1b	34.7 ± 5.7a	44.4 ± 1.9a	38.1 ± 3.8a	31.5 ± 3.2a	31.8 ± 3.0a
18	17.2 ± 8.7b	38.8 ± 3.6a	48.0 ± 1.9a	37.2 ± 3.7a	38.2 ± 3.2a	35.6 ± 3.0a
25	20.8 ± 11.8b	44.3 ± 4.7ab	48.8 ± 2.3a	46.6 ± 2.6ab	38.8 ± 3.8ab	42.9 ± 4.5ab

Means within rows followed by different letters are significantly different (Bonferroni-*t*-test; $P < 0.05$).

Table 2. *B. argentifolii* egg hatch percentages, nymph survivorship, and nymph percentages that developed to a particular stage on Teflon membranes after removal from *G. hirsutum* that was maintained under long-day conditions for an extended period (LD:LE), under long-day conditions only during the oviposition period (LD:SE) or under short-day conditions for an extended period (SD:LE)

Counts, d	Treatment (mean[a] ± SEM)			ANOVA		
	LD:LE	LD:SE	SD:LE	*F*	df	*P*
			Egg hatch			
6	75.4 ± 1.7a	69.8 ± 1.6a	57.0 ± 2.9b	19.4	2, 45	<0.0001
			Survivorship			
6	77.3 ± 1.2a	79.0 ± 1.0a	69.1 ± 1.5b	18.5	2, 45	<0.0001
14	74.6 ± 1.3a	74.2 ± 1.4a	63.4 ± 2.2b	13.8	2, 37	<0.0001
20	74.8 ± 2.5a	73.7 ± 1.2a	64.4 ± 2.2b	8.9	2, 34	<0.001
			Development			
6[b]	74.4 ± 2.9a	82.8 ± 1.6b	82.1 ± 1.6b	4.8	2, 45	<0.05
14	55.8 ± 2.6a	46.0 ± 2.9a	51.2 ± 3.4a	2.4	2, 37	NS
20	61.7 ± 3.4a	55.1 ± 3.2a	60.9 ± 4.1a	1.0	2, 35	NS

Means within rows followed by different letters are significantly different (Bonferroni-*t*-test).
[a] Combined results for two trials.
[b] Values for 6-d counts are based on percentage of nymphs that are first instar; values for 14- and 20-d counts are based on the percentage of nymphs that have reached the third or fourth stadium or adult stage.

Discussion

We found that both biotic and abiotic factors influenced hatch rates of eggs that were placed on the artificial feeding chambers. The differences that we observed demonstrate that there is an important egg/plant interaction, because once eggs were removed from the plant tissue and placed on the membranes, conditions were the same for all treatments. Whitefly eggs possess a pedicel, which is a peglike extension of the chorion. The pedicel secures the eggs to the host plant, and is inserted either into a slit made by the ovipositor in the leaf surface or into a stomatal opening. Of the 14 species that have been examined, only *B. tabaci* and *Trialeurodes vaporariorum* (Westwood) insert their eggs directly into leaf tissue (Paulson and Beardsley 1985). In 1931, Weber (Weber 1931) postulated that water passed osmotically into the egg through the pedicel. Paulson and Beardsley (1985) also thought that moisture was absorbed through the pedicel and was required for normal development of the egg. This was not proven empirically, however, until Byrne et al. (1990) assayed eggs of *T. vaporariorum* raised on plants irrigated with tritiated water. They demonstrated that fluids extracted from plant tissue accounted for ≈50% of the mass of the mature whitefly egg. A substantial increase in mass occurred within 4 h and reached a plateau 24 h after oviposition. More recently, Buckner et al. (2002) have provided additional evidence that demonstrates that both *B. tabaci* and *T. vaporariorum* eggs take up water and water-soluble solutes via the pedicel.

Our finding that younger eggs had a reduced hatch in comparison with 5- and 6-d-old eggs suggests that either development was not sufficiently advanced or that the fluids taken up from the plant were insufficient to enable a normal hatch. For eggs, like those of *B. argentifolii* and *B. tabaci*, which normally take 5–7 d to complete development (Powell and Bellows 1992, Tsai and Wang 1996, Yee and Toscano 1996), certain embryonic events are just beginning or have not yet occurred at 3 d (i.e., dorsal closure, imaginal discs invaginate, larval cuticle forms, synapses develop, motor axons grow and muscles develop) (Chapman 1998). Alternatively, it is possible that the chorion was

Table 3. *B. argentifolii* egg hatch percentages, nymph survivorship, and nymph percentages that developed to a particular stage on Teflon membranes after removal from *G. hirsutum* that was maintained under high light intensity (≈36,000 lux) or low light intensity (≈10,000 lux) with a photoperiod of 14:10 (L:D) h

Counts, d	Treatment (mean[a] ± SEM)		ANOVA		
	High light intensity	Low light intensity	*F*	df	*P*
		Egg hatch			
7	77.5 ± 1.0a	68.7 ± 1.1b	34.1	1, 38	<0.0001
		Survivorship			
7	75.3 ± 0.9a	72.7 ± 1.2a	3.0	1, 38	NS
14	74.3 ± 1.1a	72.8 ± 1.2a	0.8	1, 38	NS
21	75.1 ± 1.2a	73.3 ± 1.6a	0.7	1, 37	NS
		Development			
7[b]	45.1 ± 2.1a	42.6 ± 2.0a	0.7	1, 38	NS
14	53.7 ± 1.4a	55.3 ± 1.7a	0.5	1, 38	NS
21	58.0 ± 1.4a	58.3 ± 1.3a	0.1	1, 37	NS

Means within rows followed by different letters are significantly different (Bonferroni-*t*-test).
[a] Combined results for two trials
[b] Values for 7-d counts are based on percentage of nymphs that are first instar; values for 14- and 21-d counts are based on the percentage of nymphs that have reached the third or fourth stadium or adult stage.

not fully developed in these younger eggs and our manipulations may have damaged the embryo.

The hatch rates for 8- and 9-d-old eggs were also reduced in comparison with 5- and 6-d-old eggs. In this case, many of the eggs had already hatched at the time of collection. Those eggs that remained on the plant were less likely to hatch, the nymphs that emerged had reduced survival, and although not significantly different, there was a slight reduction in percentage of nymphs that progressed beyond the third stadium, when compared with nymphs from 5- and 6-d-old eggs. These eggs did not appear desiccated when they were transferred, so some other factor that we cannot account for is probably responsible for the reduced viability of these eggs.

We also found that long-day and high light intensity treatments during the oviposition period significantly enhanced percent hatch of *B. argentifolii* eggs when compared with short-day and low light intensity treatments. Additionally, nymphs from eggs oviposited under long-day conditions survived better through day 20 and progressed to the second stadium at day 6 more often than nymphs reared under short-day conditions. Whether oviposition occurred on plants that were kept under long-day conditions or that were transferred back to short-day conditions for 5–6 d after the 24-h oviposition period, seemed to have little effect on hatch rates and survival. The initial 24 h after oviposition, when eggs were held under long-day conditions, was sufficient for eggs to benefit from the higher photosynthetic rates that are induced by longer days.

Similar to our findings, El-Helaly et al. (1971, 1977) showed that *B. tabaci* completed their development significantly faster under long-day conditions (16:8 [L:D] h) when compared with short-day conditions (8:16 [L:D] h). The developmental time from egg to adult was ≈18 d under long-day conditions and 28 d under short-day conditions. Argov et al. (1999) found a comparable response in the citrus whitefly, *Dialeurodes citri* (Ashmead), where development was slower under a photoperiod of 12:12 (L:D) h than 16:8 (L:D) h.

This report demonstrates that daylength and light intensity have a significant impact on *B. argentifolii* egg/plant interactions. Furthermore, we showed that when *B. argentifolii* eggs were removed from the plant tissue and placed on an artificial feeding system, the subsequent development and survival of whitefly nymphs was altered by the lighting conditions during oviposition. How these conditions are influencing either the adult female during oviposition or the eggs during embryonic development warrants additional studies.

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